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Perceived Contrast Following Adaptation to Gratings of Different Orientations

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Using a contrast matching procedure, we measured the perceived contrast of vertical test gratings after adapting to other gratings of either vertical or horizontal orientation. The results show that both parallel and orthogonal adapting gratings reduce perceived contrast and do so proportionally more at low test contrasts than at high. The results are consistent with a single mechanism model proposed by Ross and Speed [(1991). *Proceedings of the Royal Society (Series B), 246*, 61–69] that assumes that adaptation to gratings repositions contrast-response transducer functions. They are not consistent with the notion of two different forms of adaptation, subtractive for parallel and multiplicative for orthogonal adaptors as proposed by Snowden and Hammett [(1992). *Nature, 355*, 248–250]. Nowhere is the reduction in perceived contrast by an orthogonal grating greater than that by a parallel grating of the same contrast. A direct comparison using two orthogonal adaptors confirms the greater potency of parallel adaptors, but also reveals interactions between the adaptors. Copyright © 1996 Elsevier Science Ltd.

Perceived contrast   Adaptation   Transducer functions   Adaptive shifting

INTRODUCTION

As was pointed out by Blakemore *et al.* (1973), adapting to a grating can raise the contrast thresholds of other gratings as well as decrease their apparent contrast when they are above threshold. Blakemore *et al.* (1973) suggested that the cause of both effects was a desensitization of "a particular population of feature-detecting neurones" (p. 1929), since they found that both were similarly tuned in orientation and spatial frequency. But what does it mean to say neurons are desensitized? Some neurophysiological evidence (e.g. Ohzawa *et al.*, 1985; Albrecht *et al.*, 1984) has been taken to indicate that neurons affected by adaptation reduce their response-gain, i.e. reduce the ratio of output signal to input contrast.

Georgeson (1985) has shown that the presumed reduction in response gain is subtractive in form, when the grating adapted to is similar in orientation to the grating affected by adaptation. However, Snowden and Hammett (1992) propose that there are two forms of reduction: one subtractive, that applies to gratings similar in orientation to the adapting grating; and the other multiplicative (divisive in their terminology), that applies to gratings orthogonal to the adapting grating, or nearly so. Because of this, they argue, the apparent contrast of a high-contrast grating may, under certain circumstances be decreased more by adaptation to a grating orthogonal to it than to a parallel grating of the same contrast and spatial frequency. They adduce evidence to support this surprising proposition and the related proposition that the tuning functions for threshold elevation and the decrease in apparent contrast are not, as Blakemore *et al.* (1973) argued, similar. According to Snowden and Hammett (1992) these functions are, in fact, very different.

We have suggested (Ross & Speed, 1991) that the primary effect of adaptation is to reposition contrast-response functions on the contrast axis. This repositioning can be thought of as a change in contrast-gain, as distinct from response-gain. It is more consistent with both the single-cell evidence of Ohzawa *et al.* (1985), Albrecht *et al.* (1984), Bonds (1991) and Geisler and Albrecht (1992), as well as with VEP results presented by Nelson *et al.* (1984), than is the response-gain reduction interpretation mentioned above. In all of these cases, the evidence indicates directly a shift in the operating range of neural mechanisms responsive to contrast, possibly also in conjunction with a compression of the response range. The consequences of such an adaptive shift need to be calculated via a model that includes the form of the contrast-response equation and a statement of how its position and shape parameters are altered by adaptation.

Our purpose here is to measure how much the perceived contrast of test gratings is decreased by adaptation to parallel and orthogonal gratings, to

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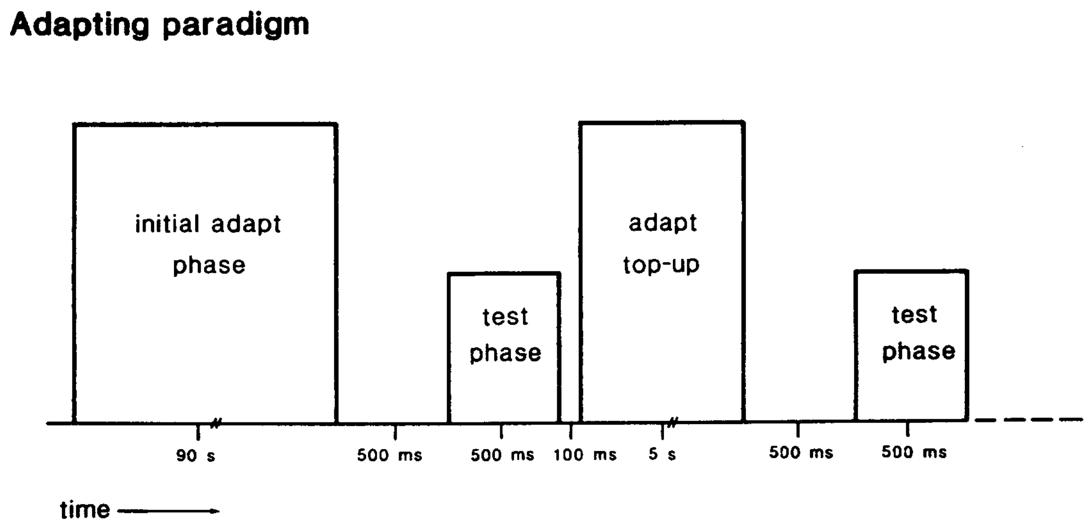

FIGURE 1. Schematic summary of temporal aspects of the adapt–test regime used in Experiment 1.

determine if parallel and orthogonal gratings have effects of different or of similar kinds and to test the accuracy of calculations based on a model (Ross & Speed, 1991) of the effects of adaptation on contrast-response functions.

METHOD

In all experiments, the adapting and test stimuli were sinusoidal gratings reversed periodically in contrast (square-wave reversal) at a rate of 2 or 4 Hz. Gratings were generated by and displayed on the screen of a SUN 4/110 workstation at contrasts defined as the Michelson ratio: $(L_{max} - L_{min})/(L_{max} + L_{min})$. Resolution of an effective 11 bits was achieved by bit stealing, i.e., by incrementing separately the intensity of each of the three colour guns of the display to create additional steps of slightly different hue between adjacent gray levels. The display characteristics of the screen were highly linear over the full range of contrasts employed. All gratings had a mean luminance of 20 cd/m^2 and were presented on a 30 × 20 cm background field of the same mean luminance. Measurements were made in a semi-darkened room while observers fixated binocularly on a central spot on the display at a viewing distance of 114 cm. All measurements were carried out in detail for one of the authors (HS) and the main results were confirmed by at least one other observer.

The perceived contrast of vertical gratings affected by adaptation was determined using a contrast matching procedure. In the first experiment, the adapting and test gratings were all 2 cpd, reversed in contrast at a rate of 4 Hz. An adapting grating measuring 6.5 × 6.5 deg was centred on a point 3.6 deg to one side of the central fixation point, and a blank field of the same size and same mean luminance as the adapting stimulus was placed symmetrically on the other side. After viewing the adapting grating for 90 sec the observer was presented with two vertical gratings of the same field size: one a comparison grating where the blank field had been positioned and the other a test grating where the adapting grating had been. The two gratings appeared simultaneously for 500 msec and the observer adjusted either (1) the contrast of the unadapted comparison grating to match that of the adapted test; or (2) the contrast of the adapted test to match that of the unadapted comparison. Grating contrast could be incremented or decremented in either small (0.5 dB) or large (5 dB) steps. After each contrast adjustment, a 5 sec "top up" period of adaptation was presented before the two gratings appeared next. To avoid any possible sequential masking effects due to the adapting grating (Foley & Yang, 1991; Foley & Boynton, 1993), the adapting and testing phases were separated by a 500 msec presentation of the uniform background field. The procedure (shown schematically in Fig. 1) ended after eight contrast reversals, with the mean of the last five reversals being taken as the perceived contrast match. Typically, each measurement was obtained in less than 20 trials.

The adapting grating was oriented either the same as the test (vertical) or orthogonal to it (horizontal). Both adaptors were presented at four contrast levels: 20, 50, 70 and 90%. Within a single session, adaptor orientation and contrast were both fixed and the adapt–test procedure was repeated for test gratings of different contrasts, within the range 2–90%. Contrast presentation was ordered from low to high. The initial contrast of the comparison grating was reset randomly (under computer control) from one measurement to the next, to within ± 2 dB of the test contrast. A 30 min rest period was provided between sessions. Prior to any adaptation, matches to 2 cpd vertical gratings of different contrasts were determined using the same procedure, the adapting gratings being replaced by a uniform field of the same mean luminance.

In a separate experimental session, the adapting stimulus consisted of two gratings: a vertical grating of 50% contrast displayed on one side of the fixation point and a horizontal grating of the same contrast displayed simultaneously on the other side. Both the adapting and test gratings had the same spatial and temporal config-

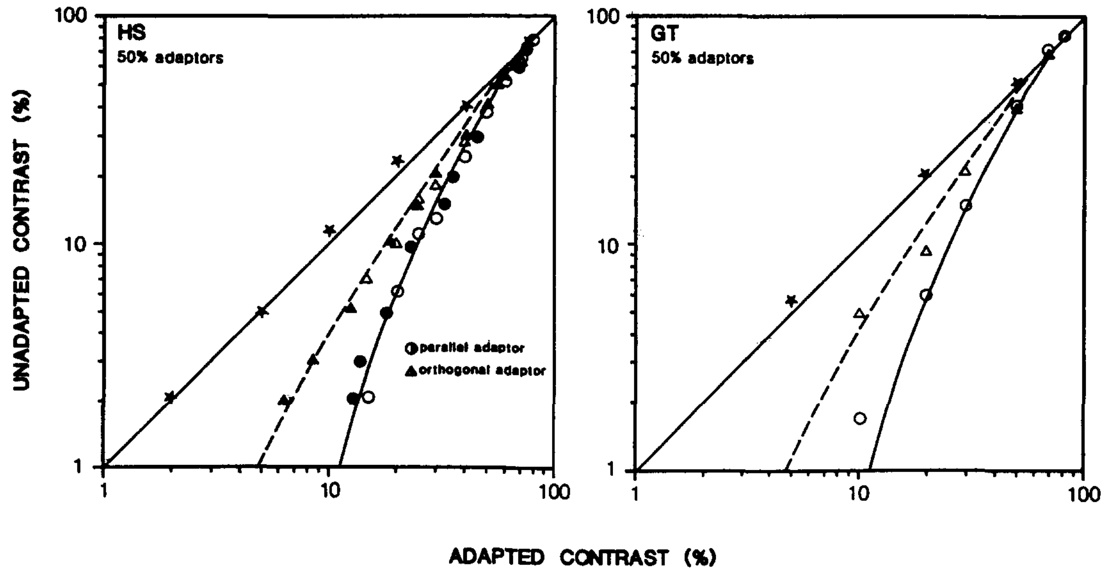

FIGURE 2. Perceived contrast of vertical test gratings following adaptation to parallel (circles) and orthogonal (triangles) oriented gratings at 50% contrast. All gratings were 2 cpd, contrast-reversed at 4 Hz. Each data point is the mean of five contrast matches for observer HS (left panel) and three matches for GT (right panel). The lines of unit slope indicate no effect of adaptation on perceived contrast. The star symbols around this line are control measurements in the unadapted condition. Data were obtained in two ways: by adjusting the contrast of an unadapted comparison grating to match that of the adapted test (open symbols) and by adjusting the adapted test to match that of the unadapted comparison grating (solid symbols). Curves drawn through the data are derived from a model by Ross and Speed (1991).

urations as those used for single-adaptor measurements. The adapt–test procedures were also the same, except that for these measurements, observers adjusted the contrast of the grating affected by an orthogonal adaptor to match that of the grating affected by a parallel adaptor, or did the reverse: they adjusted the parallel adapted grating to match the contrast of the orthogonal adapted grating.

In a second experiment, we repeated the single-adaptor measurements of the first experiment using adapting and testing conditions similar to those used by Snowden and Hammett (1992). For these measurements, the adapting and test gratings were 5 cpd, reversed in contrast at a rate of 2 Hz. Mean luminance remained at 20 cd/m^2. The adapting field measured 5 × 5 deg, centred 3.5 deg to the right of the central fixation point at a viewing distance of 114 cm. The two test fields were smaller than the adapting field, measuring 3 × 3 deg and centred 3.5 deg either side of the fixation point. As in the first experiment, adapting gratings were oriented either the same as the test gratings, or were oriented orthogonally to them. The contrast of both adaptors was fixed at 60%. The initial period of adaptation was 60 sec, with top-up periods of 6 sec between each contrast adjustment. The adapt–test regime was otherwise the same as the previous experiment.

RESULTS

Figures 2 and 3 show the perceived contrast of vertical gratings after adaptation to other gratings of vertical (circles) or horizontal (triangles) orientation. For these measurements, all gratings were 2 cpd, contrast-reversed at 4 Hz, with both the adapting and test fields of identical size (6.5 × 6.5 deg). Figure 2 plots data obtained with adaptors of 50% contrast for two observers, HS and GT. Figure 3 shows, for one observer (HS), the effects of parallel and orthogonal adaptors at four different contrasts: 20, 50 (re-plotted from Fig. 2), 70 and 90%. Perceived contrast was measured in two ways: firstly, by adjusting the contrast of an unadapted grating until it matched that of the adapted grating (open symbols) and secondly, by adjusting the contrast of the adapted grating until it matched that of the unadapted one (solid symbols). The first is our preferred method, but the second is the one used more often. Note that both methods give very similar results.

The lines of unit slope in both figures represent no loss of apparent contrast and the data points around this line (Fig. 2; stars) are control measurements made in the absence of prior adaptation. Points below this line show by how much the contrast of an unadapted grating needs to be reduced in order to match the apparent contrast of a grating as reduced by adaptation. Curves through the data points are fitted by eye, except in the 50% adaptor panels (both figures) where they are derived from a model (see Discussion). Two observations stand out immediately: (1) proportional effects reduce as test contrast increases (all curves converge toward the line of no effect and intersect at a test contrast near the adapting level); and (2) the effects of parallel adaptors are never less than those of orthogonal adaptors of the same contrast. The parallel and orthogonal curves converge as adapting contrast increases and as the test contrast increases. At low test and moderate adapting contrasts, where effects are large, it is invariably the parallel adaptors that have the larger effects. A third general observation of the data

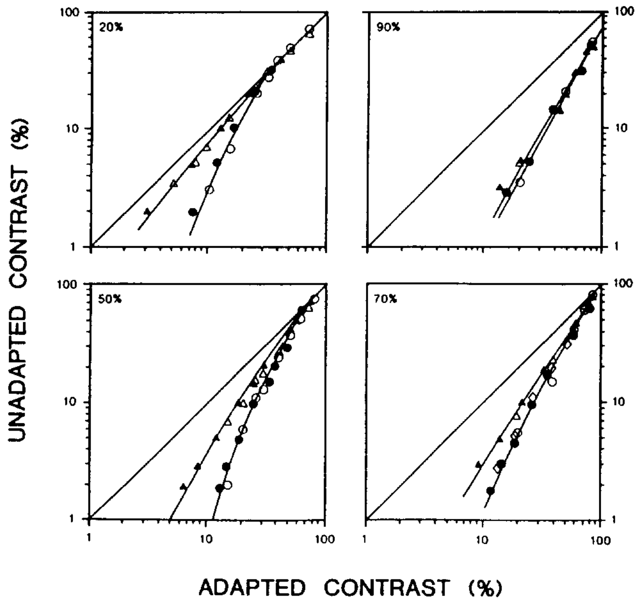

FIGURE 3. The effects of parallel and orthogonal adaptors at four different contrast levels: 20, 50, 70 and 90%. All data are for observer HS and are plotted as for Fig. 2. Curves drawn through the data are by eye, except those for 50% adaptors (re-plotted from Fig. 2), which are derived from a model. Diamond symbols displayed in the 70% adaptor panel are data replotted from Blakemore *et al.* (1973, Fig. 4), who adapted (at 70% contrast) and tested with stationary vertical gratings of 8.4 cpd.

in Fig. 3 is that as adapting contrast increases, so the orientation selectivity of the contrast reduction effect reduces progressively until, at 90% adapting contrast, it is absent.

As a more direct comparison between the effects of parallel and orthogonal adaptors, vertical and horizontal gratings of 50% contrast were displayed side by side as adaptors, then replaced by two vertical test gratings. Figure 4 shows the results of matching perceived contrasts by adjusting the contrast (1) of the grating affected by orthogonal adaptation (open symbols); and (2) of the grating affected by parallel adaptation (solid symbols). For this figure, data below the line of unit slope (equal effect) indicate the amount by which the contrast of the orthogonally adapted grating must be reduced to match the apparent contrast of the parallel adapted grating. Since all the points fall below the line of equal effect, or on it, this direct comparison confirms that parallel adaptation never has an effect less than that of orthogonal adaptation.

In the course of making matches, we noticed that adaptation changes aspects of test gratings other than their contrast. There are changes in overall brightness, parallel adaptation (lowering the overall brightness of a grating) and orthogonal adaptation (raising it). These changes in brightness complicate the measurement of apparent contrast. In making our main measurements, our matching criterion was an impression of the overall contrast of test and comparison gratings, ignoring differences between them in the brightness of their light or dark bars. We satisfied ourselves in control experiments that, using this criterion, we could make accurate contrast matches between two gratings of different mean luminance (and thus of different bar brightnesses) when neither one was affected by adaptation (see also Kulikowski, 1976; Peli *et al.*, 1991).

When we deliberately ignored overall contrast and matched, instead, the apparent darkness of the dark bars of gratings unaffected by adaptation to that of the dark bars of gratings so affected, our results, (shown in Fig. 5) were different and closer to those of Snowden and

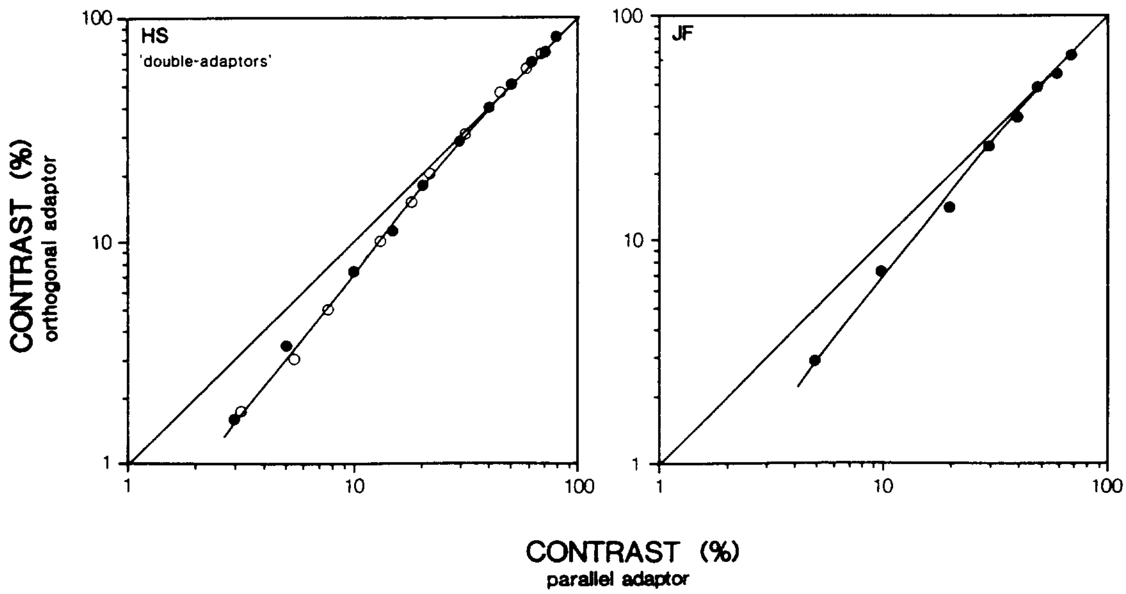

FIGURE 4. The effects of simultaneous side-by-side adaptation to parallel and orthogonal gratings of 50% contrast on the perceived contrast of vertical test gratings. The data are plotted as in Fig. 2. Data were obtained either by adjusting the contrast of the test grating affected by parallel adaptation (solid symbols) or by adjusting the contrast of the grating affected by orthogonal adaptation (open symbols). Curves fitted to the data are by eye.

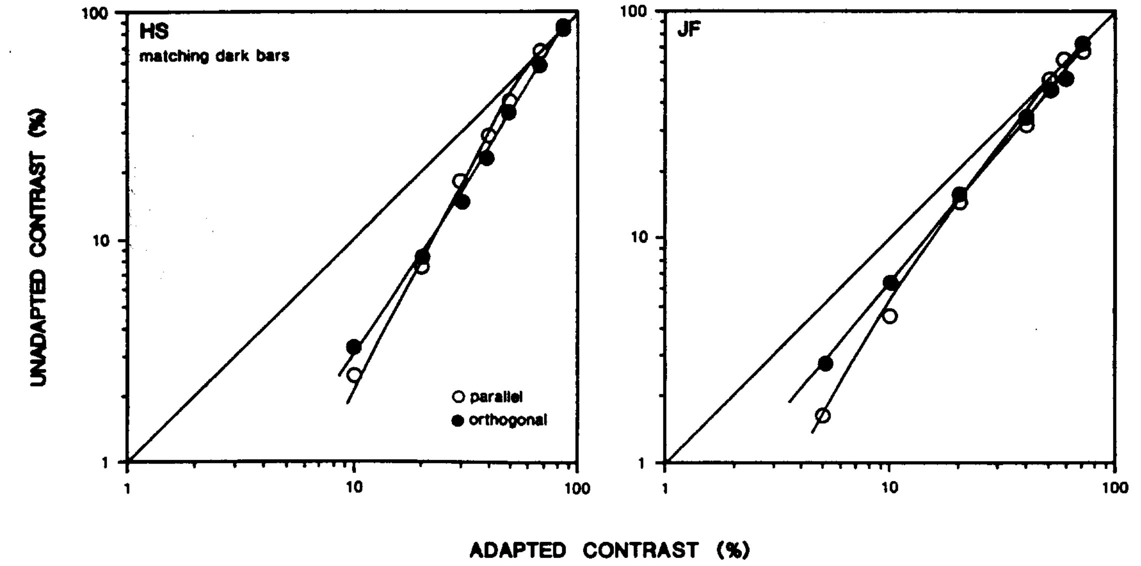

FIGURE 5. Perceived contrast measured by matching the apparent darkness of the dark bars of gratings unaffected by adaptation to that of the dark bars of gratings affected by either parallel (open circles) or orthogonal (solid circles) adaptors. The adapting and test gratings were the same as those described for Fig. 2. Adaptor contrast was 50%. Data points are the mean of five matches for HS and three for JF.

Hammett (1992). Using this dark bar criterion, we found that a 50% orthogonal adaptor seemed to reduce the contrast of a high-contrast test slightly more than did a parallel adaptor. This is explicable if parallel adaptors reduce overall brightness and orthogonal adaptors raise it. However, perceived contrast curves, both for parallel and orthogonal adaptors, still joined the line of no effect as in Fig. 2 and thus, even with the darkness matching criterion, we found no evidence for multiplicative adaptive effects in the orthogonal case compared with subtractive effects in the parallel.

There are other, more subtle, effects of adaptation. When contrast is matched, the light bars of gratings affected by parallel adaptation appear broader than the bars of comparison gratings and those of gratings affected by orthogonal gratings appear narrower. These size effects are most pronounced at low test contrasts, where, without any adaptation, light bars appear broader than dark bars (Chan *et al.*, 1992). There is also slight change in hue, towards yellow after parallel adaptation and towards blue after orthogonal (*cf* Whittle and Challands, 1969). Also, after both parallel adaptation and orthogonal adaptation, an affected grating looks more lustrous, as if there were a veiling sheen.

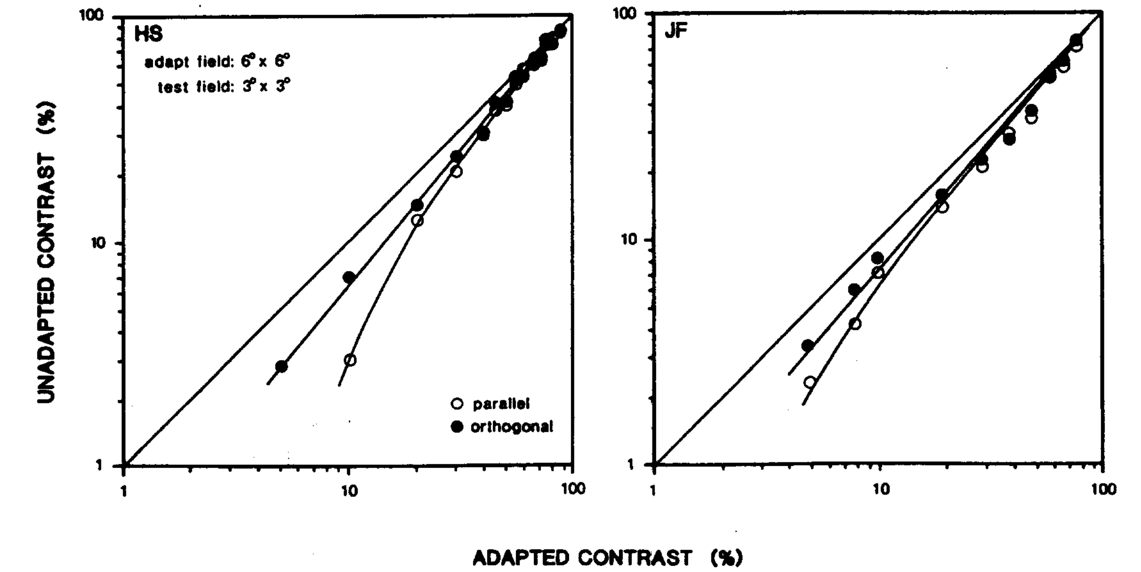

FIGURE 6. Contrast matches under conditions similar to those used by Snowden and Hammett (1992). Observers adapted for 60 sec to gratings oriented either vertically or horizontally at 60% contrast and then matched contrasts for vertical test gratings at contrasts within the range 0.5–60%. Adapt and test gratings were both 5 c/deg, but test gratings were of smaller field size (3 × 3 deg) than the adapting field (5 × 5 deg). All gratings were contrast-reversed at 2 Hz. Mean luminance remained 20 cd/m^2.

To be sure that the pattern of results described above was not peculiar to the experimental conditions chosen, we repeated the main experiment, using stimuli and procedures similar to those used by Snowden and Hammett (1992). For these measurements, test fields (3 × 3 deg) were smaller than adapting fields (5 × 5 deg) and adaptor contrast was 60%. The data so obtained, shown in Fig. 6, are consistent with the results of the previous experiment (Figs 2–4). Nowhere is the reduction in perceived contrast by the orthogonal adaptor greater than that by the parallel adaptor. The two curves converge as test contrast is increased and together intercept the line of no effect at a contrast near the adapting level.

DISCUSSION

The effects we find for parallel adaptation are very similar to those reported by Blakemore *et al.* (1973) and Georgeson (1985). Indeed, as the 70% panel in Fig. 3 shows, our results and those of Blakemore *et al.* (1973) (open diamonds) agree very closely for the case of a parallel adapting grating at 70% contrast. This is despite differences in the spatial and temporal parameters used in their experiment and ours.

Like both Blakemore *et al.* (1973) and Georgeson (1985), we find that adapting effects diminish with increasing test contrast and that there is little change in apparent contrast at test contrasts above the adapting level. As Georgeson points out, the pattern he found broadly resembles what would be predicted if adaptation had a constant subtractive effect. But the resemblance is only crude; curves would not join the line of no effect as they do, both in his data and ours, if adaptation subtracted a constant from a test grating at every level of contrast.

Blakemore *et al.* (1973) found no significant change to perceived contrast following adaptation to a grating oriented 45 deg from the test. Although they did not test the orthogonal condition, their result gave rise to the view of a simple orientation-tuned effect. Furthermore, the similarity of tuning for threshold elevation and for loss of perceived contrast led them to infer the same mechanism underlying both effects: the elevation in threshold being "merely a special case of apparent contrast reduction" (p. 1927).

Recently, however, Snowden and Hammett (1992) reported conditions under which an orthogonal adaptor not only can reduce the perceived contrast of a test pattern, but, at appropriate test contrasts, can do so more than a parallel adaptor of the same contrast. These authors contrast matched vertical test gratings at contrasts within the range 0.5–60% after adapting for 60 sec to either parallel or orthogonal gratings at 60% contrast. The adapting and test gratings were both 5 c/deg, but they differed in field size (5 deg adapt field, 3 deg test field). They found that both parallel and orthogonal adaptors reduced perceived test contrast; however, whereas the parallel adaptor curve converged toward the line of no effect as test contrast increased, the orthogonal adaptor curve ran parallel to it exhibiting, at high test contrasts, a reduction in perceived contrast where parallel adaptors had caused none. These results led Snowden and Hammett to conclude, firstly, that adaptation effects on threshold contrast and on apparent contrast are tuned differently, at least in the orientation domain; and secondly, that orthogonal and parallel gratings have qualitatively different kinds of adaptive effect on apparent contrast: parallel gratings having a subtractive effect and orthogonal gratings having a multiplicative effect.

We find also that adaptors oriented orthogonal to the test can reduce perceived contrast, particularly when the grating affected by adaptation is at low contrast. However, unlike the data of Snowden and Hammett, we find a pattern of convergence to the line of no effect for orthogonal as well as for parallel adaptation; and that parallel adaptation has the greater effect, except at the highest level of adaptation, 90% contrast. Here the effects of parallel and orthogonal gratings are virtually identical. Pitting parallel against orthogonal adaptors (side-by-side gratings of different orientation) confirms that parallel adaptors always have effects that are either as great as, or greater than, orthogonal adaptors of the same contrast. We, therefore, find no evidence that orthogonal and parallel gratings have different kinds of adaptive effect, as well as no evidence that orthogonal gratings ever have greater effects than parallel gratings, even when experimental conditions resemble closely those used by Snowden and Hammett. In particular, we do not find that the curves for orthogonal adaptation in Fig. 3 run parallel to the line of no effect, as the hypothesis of a multiplicative (or divisive) effect of adaptation on response-gain would require them to do on log–log coordinates.

Thus, a multiplicative hypothesis can be rejected as an explanation for any part of our data, but so, too, can the subtractive hypothesis, since all curves in Fig. 3, except those in the 90% panel, join the line of no effect when test contrast is a little above the adapting contrast. The subtractive hypothesis requires that curves converge toward the line of no effect on a log–log plot, but that they never join it.

Ross and Speed (1991) suggested that contrast-response curves obey a form of the Naka–Rushton equation (Naka & Rushton, 1966), $R = C^n/(C^n + C_{50}{}^n$ and that adaptation both shifts the semi-saturation constant, C_{50} and changes the exponent, n. This model of the effects of adaptation was developed to explain threshold elevation, but it can be applied to apparent contrast by assuming that apparent contrast is proportional to R, the response to input contrast C, in the model. The idea that the model may also explain the reduction of the apparent contrast of suprathreshold gratings, as well as changes in thresholds as a result of adaptation, is supported by the modelling illustrated in the 50% panel of Figs 2 and 3. These curves are not lines fitted by eye to the data, as they are in the other panels, but are predictions made by assuming apparent contrast to be proportional to R in the model. Parameter values used are

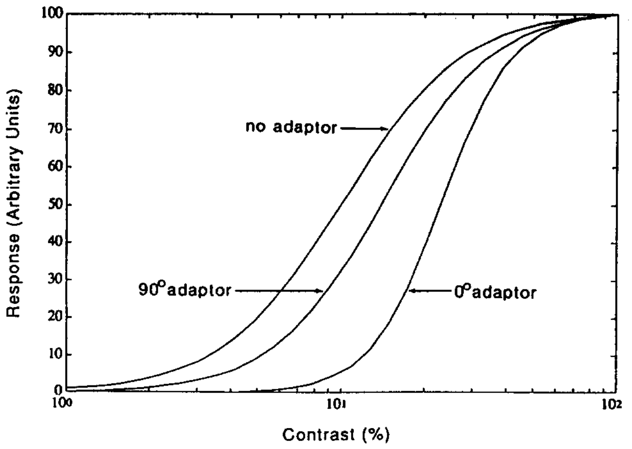

FIGURE 7. Model contrast transducer functions of the generalized Naka–Rushton form used to calculate theoretical curves fitted to the data for 50% contrast adaptors in Figs 2 and 3. Shown in the figure are transducer functions before adaptation (no adapt) and after adapting to either an orthogonal grating (90 deg adaptor) or parallel grating (0 deg adaptor). Parameter values used to generate these functions are: prior to adaptation, $n = 2.0$, $C_{50} = 10$; for orthogonal adaptor, $n = 2.2$, $C_{50} = 14$ and for parallel adaptor, $n = 3.4$, $C_{50} = 23$. Notice that all three curves converge at high input contrasts.

shown in Fig. 7, along with the resulting transducer functions.

The comparison contrast of a test after adaptation to a 50% contrast adaptor was calculated from the theoretical transducer functions shown in Fig. 7. For each test contrast, the predicted response was calculated, using the appropriate transducer function (0 or 90 deg adaptor) and then the no-adaptor transducer function was used to find the comparison contrast that gave the same response. It might be noted that the convergence of all functions at high contrast explains why effects for different adapting conditions are similar at high contrast although different at low.

The closeness of the fits of model predictions to the data in the 50% adaptor panels indicates that results only loosely in agreement with a subtractive hypothesis fit more closely the hypothesis of a lateral transducer shift, with compensatory changes in slope parameters. We claim no more than that this is indicative of the plausibility that this type of model explains changes in apparent contrast as a result of adaptation. We cannot claim that Ross and Speed's (1991) model, as it stands, explains both threshold elevation and apparent contrast loss. To fit contrast loss data, different parameters are needed from those that were required to explain threshold elevation (see Ross & Speed, 1991). This may indicate that the form of the transducer function needs to be changed in the model, that the relationship of proportionality between perceived contrast and response to contrast does not hold (there may be non-linearities above threshold), or that a single mechanism model, adequate for threshold elevation, breaks down at high contrast levels. And the model cannot explain why at 90% contrast parallel and orthogonal adaptors have identical effects, since it assumes greater effects for parallel adaptors at all contrasts. To do so, it would need to incorporate some limit beyond which transducers cannot be shifted by adaptation. For all these reasons, we have not attempted to fit all our data to model predictions and we regard the fits in Figs 2 and 3 merely as indicating the possibility that a model incorporating the assumption of lateral transducer shift could be developed to explain the loss of apparent contrast following adaptation.

In addition to the effects on apparent contrast, discussed above, adaptation causes other, more subtle changes in the appearance of an affected grating. There are changes in the overall brightness of gratings and in the apparent size of bars, and slight changes in hue, towards yellow after parallel adaptation, and towards blue after orthogonal. Also, after both parallel adaptation and orthogonal adaptation, an affected grating looks more lustrous. Lustre is often a sign of rivalry within the visual system (Burr *et al.*, 1986), and may be so here if the functional properties of some mechanisms are altered by adaptation but those of others are not. Evidently, much more happens in the visual system as a result of adaptation to a grating than can be captured by a model of lateral shifts of contrast transducer functions or a change in their response range. Presumably, it is to these wider effects, to the possibility of spatial spread of adaptation and to interactions between adapting gratings side-by-side (see Cannon & Fullenkamp, 1991) that we must look to understand the anomalies in our results.

Finally, we have conducted preliminary studies of the effects of masking on apparent contrast using stereo disparity to separate masks from test gratings, a suggestion for which we thank P. Whittle (personal communication). These studies indicate that masks and adaptors have qualitatively similar effects on apparent contrast.

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